7. Ecosystem Complexity in Time and Space

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7.1. GENERAL CONSIDERATIONS

Ecology deals with the relation of organisms and their environment, defined very broadly to include both biotic and abiotic aspects. Ecologists study such processes as exchanges of energy and materials between organisms and their surroundings, growth and regulation of species populations, competition between individuals of the same or different species for energy and materials, and parasitism and predation. According to ecological theory these processes have an organizing function, so that the characteristics of the population, community, and ecosystem result from the interactions among organisms and between organisms and the environment

The subject matter of ecology is much more diffuse than the subject matter of molecular, cellular, or organismic biology that deal with well defined and well delimited levels of organization, such as molecules, cells, tissues, or individual organisms. Ecology deals with sets of organisms, populations, species, communities and their relations to each other and to the surroundings environment. Physics, chemistry, molecular biology, and astronomy also deal with the interactions of units with their surrounding environment. However the "species" of the ecologists (i.e. taxonomic species as opposed to atoms, or molecules, or stars) are larger in kind and more complex in structure and function than those dealt with by other scientists (Bonner 1988). Ecosystems are one of the most intricate natural assemblies identified by humans in their quest to understand the functioning of the biosphere.

The complexity of ecosystems arises from (1) the great diversity of entities and interrelationships that comprise an ecosystems, (2) the intricate dynamics of these entities, and (3) their pattern in space. Ecosystems comprise organisms of very diverse sizes from bacteria to whales; a highly diverse and elaborate soil structure; energy, water, and nutrient fluxes, etc. These factors are not static

but are constantly evolving or changing, witness the very elaborate dynamics of the life cycle of species, and of energy, and nutrient flows. These entities show a complicated spatial distribution pattern which is difficult to interpret.

Because ecosystems are so complex and variable, many ecologists have questioned their reality. There are also serious problems regarding the definition and delimitation of ecosystems (see chapter 8 by di Castri). Populations, communities, and ecosystems do not have the same tangible reality of cells or organs, and more importantly do not possess well defined physical borders. Although there are problems in defining some organisms such as slime molds or clonal plants, these problems pale in relation to the problem of ascertaining precisely the limits of a plant community, or the limits of an ecosystem, which almost never have precisely defined borders. Nevertheless, it is generally assumed that a workable relation with the environment is achieved, not by individuals or even species acting independently, but by their acting in concert through the organization of their diverse capabilities, thereby constituting a communal system. Adaptation is assumed to be a collective rather than an individual process.

Early researchers treated ecosystems as complex systems involved in the transfer of energy and materials (Tansley 1939). One of the earliest concepts generated by this school was that of trophic organization (Lindeman 1942). According to this hypothesis, ecosystems are formed by at least four guilds of species: primary producers, herbivores, carnivores, and decomposers. Primary producers are photosynthetic plants that use water, nutrients, carbon dioxide, and sunlight, to synthesize organic compounds. Herbivores make a living eating plants and using the energy contained in the compounds synthesized by them. Carnivores (of which there can be more than one guild) consume herbivores (primary carnivores) or other carnivores (secondary carnivores). Finally decomposers, utilize the energy remaining in the tissues of dead bodies and reduce them to water, carbon dioxide, and elementary ions. It soon became clear that although heuristically very useful, the concept of a trophic organization of ecosystems was a great simplification. Furthermore, researchers very quickly run into the problem that because of the number and nature of the interactions it was impossible to understand precisely the behavior of each individual species in an ecosystems. The trophic organization of ecosystems is without doubt a source of ecological complexity.

The lack of agreement regarding the nature and precise organization of ecosystems has produced a diversity of study approaches. The majority of ecologists have tended to focus their attention on specific, but generally narrow, problems. This has resulted in the atomization of ecology into a number of narrowly focused disciplines, such as ecophysiology, whose practitioners are concerned with the details of the process of energy and material exchanges, such as photosynthesis or water relations; or population ecology, concerned with changes in numbers of individuals in populations and communities, and processes of competition and predation; or landscape ecology concerned with the effects of landscape patterns on the structure of the vegetation. Two traditions have developed within ecosystem ecology: the biological tradition that approaches ecology from a genetic-physiological viewpoint, emphasizing analysis of the behavior of individual units and a reductionist approach; and the functional tradition that is more concerned with energy and material transfers and emphasizes trophic levels (di Castri 1987). In general the information exchange and intellectual interchange between ecological subdisciplines within ecology is limited. The challenge today is to unify this diversity of approaches into a coherent theory.

The overspecialization of ecologists has reduced their ability to play a directing role in environmental policy and in the elaboration of management guidelines to deal with the problems associated with the widespread modification of the environment that is taking place as the result of increased levels of economic and industrial activity by human beings. The problems of the circumscription and nature of the levels and units of ecological interest, has therefore not only intellectual benefits, but it clearly also has very practical implications.

I now explore three aspects of ecological complexity. I first dwell with the problems associated with the dynamics of single species growth. I then explore some aspects of ecological complexity in space. I end with a discussion of how to deal with the large number of entities that comprise ecosystems. The vastness of the subject and space limitations determine that only salient points will be mentioned.

7.2 ECOLOGICAL COMPLEXITY IN TIME AND SPACE

All natural phenomena take place in time and space. However in many cases specific time and space can be disregarded. So for example, a body falling on the surface of the Earth can be described without paying attention to the precise site or exact time in which it takes place. Most ecological phenomena cannot be dealt with that way. Space (soil type, slope, latitude, etc.) and time (day-length, rainfall, temperature, etc.) are very crucial in determining the outcome of a given process, whether we describe it in biological (competition) or functional (energy flow) terms. In other words, ecological systems are non-linear, complex systems which are very sensitive to initial conditions (see chapter 2 by G. Nicolis). Such systems require special approaches to describe and quantify.

Ecological system are very variable. Species evolve from other species and eventually go extinct; populations of species get established in new sites and eventually also go extinct. From year to year the number of individuals in a population fluctuate, sometimes dramatically as during epidemics, and just as swiftly get reduced. Fluxes of energy between organisms and the environment vary daily and seasonally in ways that are only qualitatively predictable. These oscillations are usually interpreted as externally driven, mostly by changes in weather and resources. Increasingly, however, we are starting to realize that some, we still cannot say how much, of these oscillations are the result of interactions between individuals of the same or of different species. Increasingly the analysis of ecological systems is starting to mirror what molecular biologists are finding at the cell and molecular level (see previous five chapters) and physicists are detecting for physical entities: that extremely simple processes can lead to extremely complicated behavior. A good illustration is the conduct of species populations.

7.2.1 Models of Single Populations

The single species population or *deme* is the basic unit of ecology. Three principal factors control the growth of populations: (1) Exterior environmental agents that determine the rate of availability of resources that the population requires. (2) The demographic characteristics of the population, such as the number of offspring, the frequency of reproduction, the age structure, maximum life span, etc. (3) Interactions with other populations, both congeneric and

not, usually subsumed under the term "competition." However interactions with other populations are not necessarily always negative.

Thomas Malthus (1798; 1800) is credited with proposing the first model of population growth, known as the *exponential model*. For populations with discrete generations (i.e. where there is no overlap between generations, as for example in species of insects or ephemeral plants) the model can be represented by the following difference equation:

$$N_{t+1} = \lambda N_t$$

where N is the number of individuals in the population; λ (called the finite rate of increase) is the maximum growth rate per population; t is time; and $r = \ln \lambda$ (called the Malthusian parameter) is the compound rate of increase of the population. The Malthusian or exponential model describes unbounded exponential growth for $\lambda > 1$ ($r > 0$), or exponential decline to extinction when $\lambda < 1$ ($r < 0$). This model assumes the population has no age structure, ignores the role of exterior environmental factors, and the effect of other species.

No population can grow exponentially for very long. It soon will run out of resources. As the population increases in numbers it will reach a point at which the rate of growth will be in equilibrium with the rate of resource availability. We assume that birth and death rates are affected by resources. If we assume a fixed rate of resource availability then there will be an upper density K marking the maximum number of individuals that can be sustained with available resources. The rate of population growth in such a population will be a function of density.

$$N_{t+1} = F(N_t)$$

The function $F(N_t)$ relates the density at one generation to that in the previous one. A number of specific formulas for the function $F(N)$ have been proposed (May 1976; May and Oster 1976; May et al. 1974). Of these the most widely accepted is:

$$N_{t+1} = N_t e^r (1-N/K) \qquad (1)$$

This model known as the *logistic equation* can also be expressed as a differential equation (which implies continuous breeding)

$$dN/dt = rN (1-N/K) \qquad\qquad (2)$$

In this model, already introduced by Verlhurst in 1845, the effective per capita growth rate rN is reduced by the density factor (1-N/K). If N<K growth rate is positive; when N>K growth rate is negative.

The logistic model implies that there is an immediate effect of density on population growth, which of course is not the case. Organisms do not adjust their breeding or survival rates to the exact number of individuals in a site at every moment. However eq. 7-1 has an implicit time lag since the size of the population in generation $t+1$ is a function of population size in the previous generation. May and Oster (1976; May et al. 1974; Yodzis 1989) have explored the behavior of the logistic difference equation as r values increase. For values of r below 2 the population experiences damped oscillations as it approaches K (fig. 7-1). However for values above 2 the population becomes unstable. At this point it bifurcates (see chapter 2 for a detailed explanation of this behavior) and a stable limit cycle of period 2 ensues. With increasing values of r it bifurcates again giving rise to an infinite hierarchy of stable cycles of period 2^n (fig. 7-1). The sequence of stable cycles with period 2^n converges on a limiting parameter value $r_c = 3.102$. After this point the population equation has an infinite number of cyclic solutions, one for each integral period, but only one of them is stable at each value of $r > r_c$, that is, the system behaves chaotically.

This very simple and somewhat unrealistic model of population growth can produce very complex behavior and can lead to population dynamics which are *de facto* indistinguishable from the sample function of a random process (May 1981). Values for r for natural populations obtained empirically are however well below 2 in most instances. Since natural population oscillate in numbers the fluctuations in population size are probably driven by random environmental factors and not by the internal dynamics of the population. However, as Schaffer and Kot (1985) have pointed out, the value of the growth rate obtained from field studies is not equivalent to the r of the logistic equation because populations in the field are never free of other constraints, especially interactions with other species. The observed variations in natural population size are therefore not necessarily the result of the effect of external forces. They may reflect the operation of some deterministic, non-linear, and strictly density-dependent dynamics, in line with the conclusion reached by G. Nicolis in chapter 2 for other biological systems.
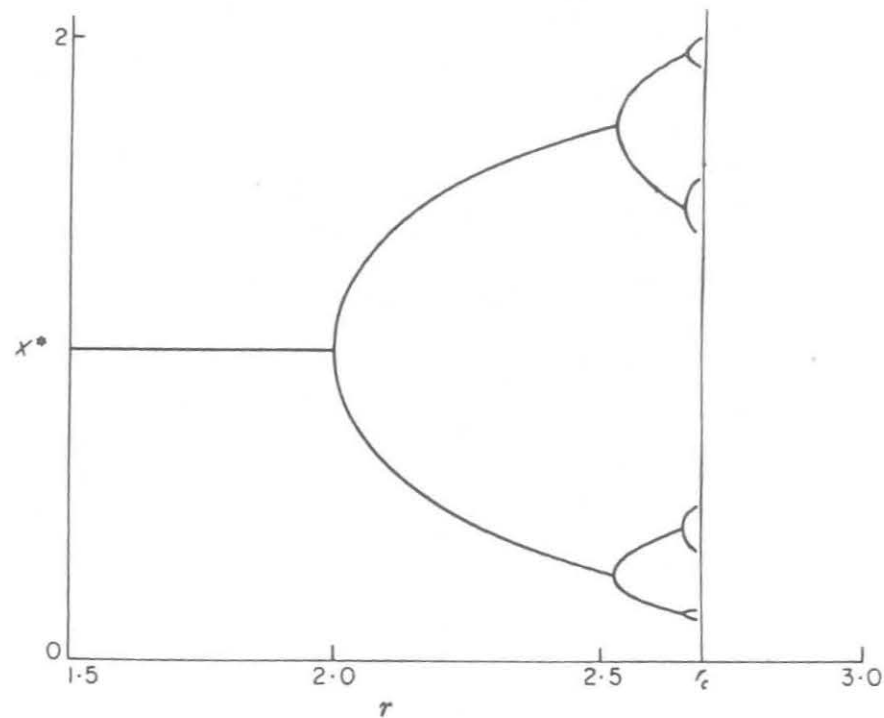
Figure 7-1. The hierarchy of stable fixed points (X^*) of periods 1, 2, 4, 8, ..., s^n (corresponding to stable cycles of periods 2^n) , which are produced by equation 7.2 . Each pair of points arises by bifurcation as a previous point becomes unstable. The sequence of stable cycles of period 2^n is bounded by the parameter value r_c; beyond this lies the chaotic region. (from May, 1981)

The logistic equation has been criticized for being overly simplistic. It can be applied solely to populations of species that breed only once and have truly non-overlapping generations (including non-dormancy of propagules) and that live in a regime where resource flux is truly fixed and shows no variation from year to year.

The logistic equation pertains either to a population with continuous breeding and complete generation overlap (eq. 7.2) or it concerns exclusively to a population with discrete breeding and absolutely no population overlap (eq. 7-1). Many plant and animal populations live for several years, and breed repeatedly. Such populations exhibit age structure and generational overlap. A realistic model must take these factors into consideration. One such model was introduced by Leslie (1945; 1959). This is a matrix model in which there are discrete age classes ($i = 1,2,3,....$, all of the same duration) of the continuous age variable x. Age class i corresponds to ages $i-1 > x$. The individuals in any age class other than the first at time $t+1$ are the survivors of the previous age class at time t

$$n_i(t+1) = P_{i-1}\, n_{i-1}(t) \qquad\qquad \text{for } i = 2,3,....$$

where P_{i-1} is the survival probability of members of age class **i-1**. Individuals of the first age class are the offspring produced by members of the population during the time interval $t - t + 1$

$$n_1(t+1) = F_1\, n_1(t) + F_2\, n_2(t) + F_3\, n_3(t) + ...$$

where F_1 is the fertility coefficient. The system of equations can be written in matrix form as follows:

$$
\begin{bmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \\ ...... \\ n_x(t+1) \end{bmatrix}
=
\begin{bmatrix} F_1\ F_2\ F_3\ ...F_x \\ P_1\ 0\ \ 0\ \ ...\ 0 \\ 0\ \ P_2\ 0\ \ ...\ 0 \\ ...\ ...\ ...\ ...\ ... \\ 0\ \ 0\ \ 0\ \ P_{x-1}\,0 \end{bmatrix}
X
\begin{bmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \\ ... \\ n_x(t) \end{bmatrix}
$$

which can be written more compactly

$$n(t+1) = A.n(t)$$

where **n** is a column vector and **A** is the transition matrix. The Leslie matrix can be generalized for stage and size structured populations (in which case we refer to it as a projection matrix), and the survivorship and fertility coefficients can incorporate density dependence. It is the basic model used by demographers (Caswell 1989).

In the density independent version the population will exhibit positive growth if the main eigenvalue $\lambda > 1$, and will decline to extinction when $\lambda < 1$. An important characteristic of this model, is that a growing population will reach a *stable age distribution*.

In a Leslie matrix with density dependence, the population will tend towards a value of $\lambda = 1$ (at which point the population is in equilibrium) with a stable age distribution. In approaching equilibrium the population undergoes a series of damped oscillations, implying the existence of a point attractor in phase space. Solbrig et al. (1988, 1990) using data from real plant populations showed however, that depending on the form of density dependence used in modelling the populations, continuous and regular oscillations ensue (Fig. 7-2) implying a limit cycle or a chaotic attractor instead.

How realistic and generalizable these models are is part of a larger discussion (but see May 1981; Holden 1986; Roughgarden, May, and Levin 1989; Yodzis 1989). Chilhood diseases (Schaffer & Kot 1986), the Canadian lynx cycle (Schaffer 1985), and outbreaks of the insect pest *Thrips imaginis* (Schaffer & Kot 1985) exhibiting low-dimensional chaotic behavior provide real world examples that give credibility to the notion that the dynamics of single population growth and reproduction is a potential source of ecological complexity.

7.2.2. Population interactions

Populations do not grow by themselves. They are embedded in a milieu in which they interact with other species, both as competitors for resources, as food for predators, or by consuming other species. Most attempts at modelling predator-prey systems have found that they oscillate.

The oldest and best known model is the Lotka-Volterra model of one predator and one prey.

$$dN_1/dt = b_1 N_1 N_2 - d_1 N_1$$

$$dN_2/dt = b_2 N_2 - d_2 N_1 N_2$$

where $n1$ and $n2$ are the sizes of the predator and prey populations and b and d are the birth and death rates of the two populations. The two populations
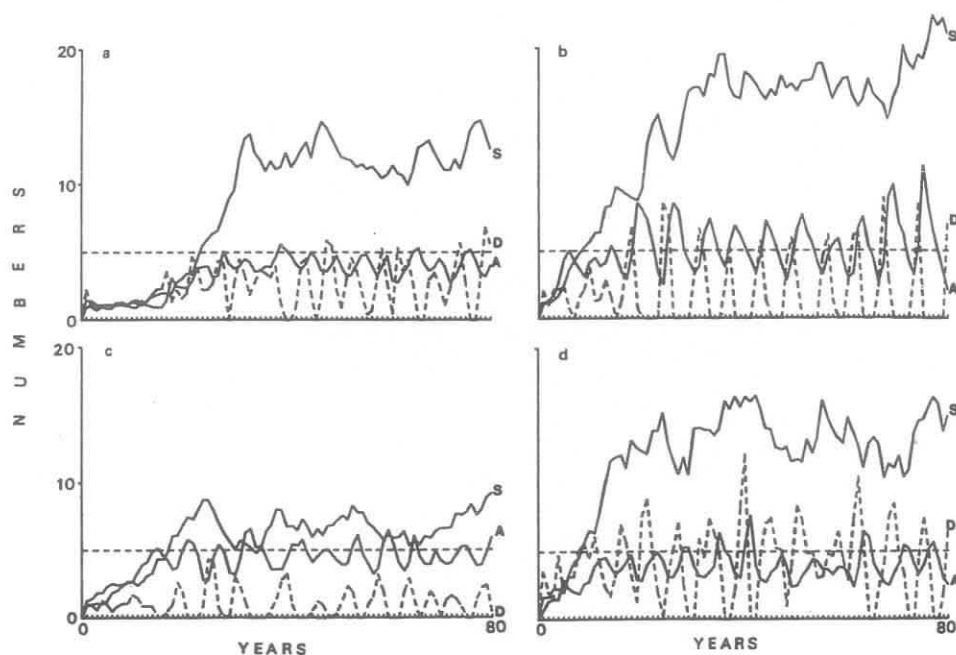
Figure 7-2. The numbers of seeds in the seed pool (**S**), seedlings (**D**), and adults (**A**) for four different computer simulations of the growth a a population of *Viola fimbriatula* for 80 generations. The scale for the ordinate is in hundreds of seedlings and adults, but in thousands for the seed pool. The dashed line at 500 adults is the density beyond which no seedlings survive. (from Solbrig, Sarandon & Bossert, 1988).

cycle with amplitude and frequency determined by initial densities (Rosenzweig and MacArthur 1963).

Gilpin (1975) studied a three species Lotka-Volterra competition community in which species 1 can exclude species 2, species 2 excludes 3, and 3 excludes 1. They can be modelled as follows:

$$dN_1/dt = r_1N_1 - [\alpha_{12} N_2 + \alpha_{13} N_3]$$
$$dN_2/dt = r_2N_2 - [\alpha_{21} N_1 + \alpha_{23} N_3]$$
$$dN_3/dt = r_3N_3 - [\alpha_{31} N_1 + \alpha_{32} N_2]$$

where N represents the size of populations 1, 2, and 3, r, their growth rates and the α_{ij} the effect that an individual of species j has on the growth rate of populations i. This can be generalizes to:

$$[1/N_i]\ dN_i/dt\ =\ r_i - \sum \alpha_{ij}\ N_j \qquad\qquad \text{for } i,j = 1,2,3$$

It can be shown, that in such as system, where species 1 and 2 may represent
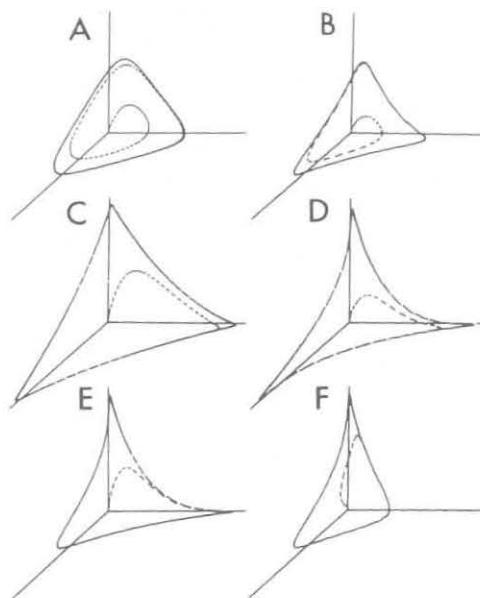

Figure 7-3. State space trajectories generated by a two prey and one predator system originally sugested by Gilpin (1979). These equations result in a Chaotic strange attractor (from Gilpin, 1979).

two herbivore species and 3 a predator that the system oscillates chaotically. This corresponds to a well defined spiral strange attractor in phase space (fig. 7-3) (Gilpin 1975; Schaffer and Kot 1986).

7.2.3. Ecological Complexity in Space

Ecological complexity may also arises from ecosystem processes occurring at different spatial scales. A terrestrial landscape is a mosaic of landforms, soil types, plant communities, agricultural fields, meadows, and artificial forests.

An emergent area of ecology is the study of the development and dynamics of these landscape patterns. Geomorphologists, soil scientists, and plant geographers among others have a long tradition of studying the origin and maintenance of landforms, soil types, and vegetation pattern. They have focused however solely on one aspect. Landscape ecology attempts to integrate this knowledge into a comprehensive theory of landscapes (Forman 1981, 1983; Forman & Godron 1986).

A landscape is a collection of patches formed by the action of geological and climatic forces; environmental disturbances resulting from both biotic and abiotic agents; the birth, death, and dispersal of organisms; and environmental constraints (Levin 1978; Urban, O'Neill & Shugart 1987). Each of these agents acts across a range of spatial and environmental scales. Geological events range from mountain building taking millions of years and affecting thousands of square kilometers to soil erosion measured in square centimeters and taking place in minutes and hours. Likewise, some species measure their life span in weeks, while others persist for decades and centuries. Furthermore the agents of pattern formation are associated in landscape development. So, for example, topographic or climatic pattern may affect the frequency of disturbances (more landslides occur the steeper the slope; fire frequency is related to both the density and quality of biomass and the climatic regime).

One of the most vexing problems faced by ecologists has been that of scale. What is the appropriate time and space scale to describe a population? a community? an ecosystem? While molecules, atoms, cells, or individual organisms have well defined boundaries in space, populations, communities, and ecosystems are much harder to limit in space. This has lead some ecologists (Gleason 1926) to deny reality to any unit above the individual. However, such a reductionist approach does not solve the problem. Humans have recognized units above the species level since time immemorial, as shown by geographical terms (taiga, savanna, pampa, cerrado, prairie) in all languages.

Quantifying the landscape heterogeneity in space is one of the scientific objectives of landscape ecology. However, the natural boundaries of landscape patches are so complex that until recently only qualitative descriptions were possible. Mandelbrot's (1977) development of fractal analysis (see chapter 2) has made it possible to quantify complex boundaries and patch shapes. Fractals allow the investigator to relate landscape patterns to the underlying process that may produce complexity (Krummel et al. 1987). I describe two applications of

fractal analysis: the relation between natural and human-made landscapes; and the reason why there are many more small organisms than large ones.

Humans have modified landscapes principally through agriculture and livestock raising, but increasingly!also through road construction, city development, and industrialization. Humans tend to create patches with characteristically simple shapes. This was demonstrated by Krummel et al. (1987) in a study of the vegetation of the Mississippi floodplain in the central region of the state of Louisiana and the southern portion of the state of Mississippi in the
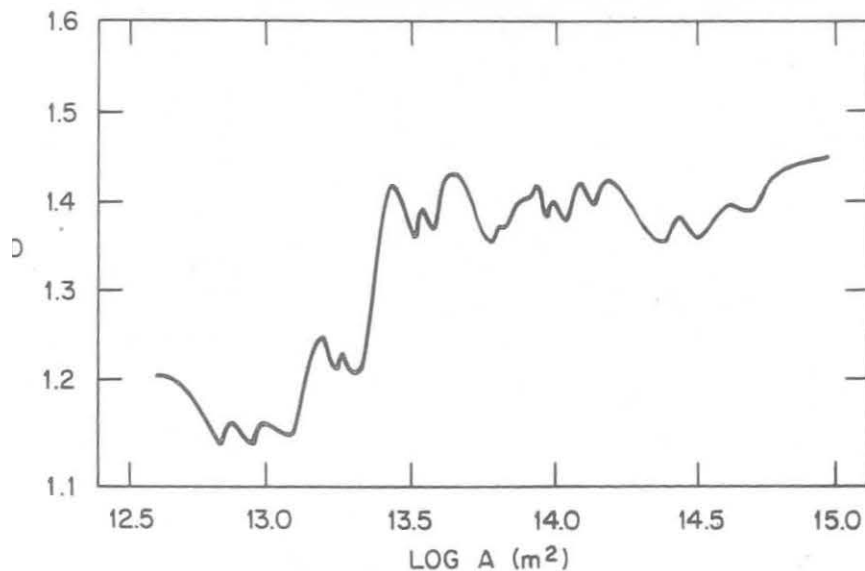

Figure 7-4. Changes in fractal dimension (D) values as the log of area (A) increases; as determined by successive regressions of the log of perimeter (P) on log of A. (from Krummel et al. 1987)

United States. They used the perimeter-area method (Mandelbrot 1977; Lovejoy 1982) to calculate the fractal dimension D of vegetation patches. They were interested in learning whether small patches had lower fractal dimensions than larger patches. This would indicate that smaller patches had smoother and more regular borders. They found a distinct break (fig. 7-4) between patches below and above 60-73 Ha. (fig. 7-5). This study shows that this technique may be of use in assessing geological, edaphological, vegetational, and anthropogenic processes operating at different spatial scales.

Direct application of this information is to the problem of the effect that breaking up the landscape into smaller and smoother patches will have on the number of animals that can exists in the remaining forest patches. This is related to the question of why in a given habitat there tend to be many more small than large animals. Morse et al. (1985) have investigated this question for insects living in habitats whose surface area are fractals. They were able to estimate that the fractal dimension **D** of the leaf surface had values between 1.3 and 1.5. Using the simple power law
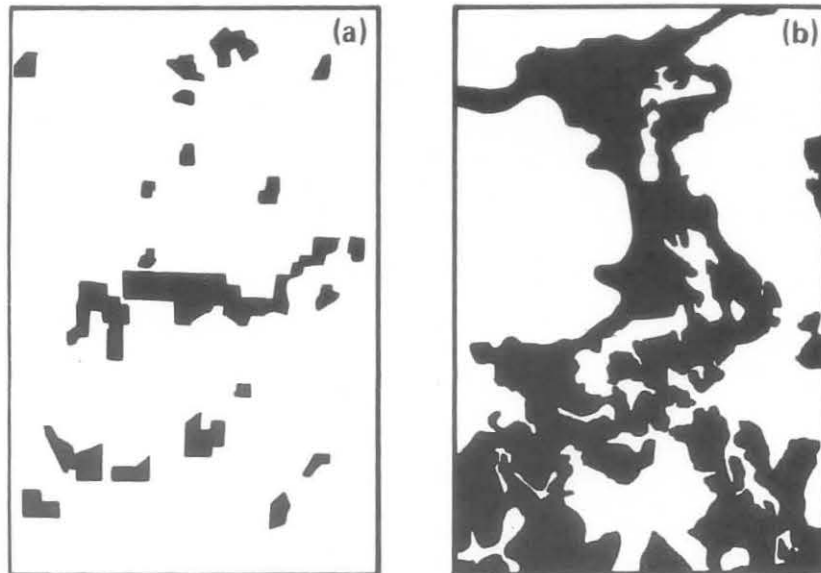

Figure 7-5. Computer plots (both at the same scale) of deciuous forest in two different areas of the Natchez Quadrangle, Mississippi, USA, showing the differences in shape complexity between small forests in the flood-plain (left) and a larger forested area on the eastern border of the floodplain (dark = forest; light = other uses) (from Krummel et al. 1987).

$$L(\delta) = K\delta^{1-D}$$

where **L** is the perimeter length measured on the characteristic scale δ, and **D** is the *fractal dimension* (2>**D**>1). Morse et al. (1985) estimated that for each order of magnitude decrease in ruler length [δ] the perceived surface area of the vegetation increases approximately between 3 and 10 times. This means that if two species of animals living on the same kind of habitat differ in size by

an order of magnitude, the smaller one would have 3 to 10 times more living space available! It indicates also that a simplification of habitats resulting in lower fractal dimensions will affect larger organisms more than smaller ones.

The spatial pattern of the vegetation affects species numbers and consequently ecosystem complexity. The concept of fractal geometry is also useful for describing the dynamic properties of fractal networks (Orbach 1986). One example is in terms of the movement of organisms in the landscape, such as agricultural pests. It has been shown (Orbach 1986) that diffusion is slowed down on a percolating network (see chapter 4 by G. Careri) compared to diffusion in Euclidean space. The larger the fractal dimension the smaller the mean square distance travelled by an organisms in a fractal network in a unit of time. Consequently, the simpler the structure of an agricultural field (lower fractal dimension) the faster a pest will be able to cover the field. For wild species that stay only within islands of native vegetation, the simplification of the landscape may have the opposite effect. It may slow considerably their migration.

7.3. COMPLEXITY OF ECOLOGICAL ENTITIES

The size distribution of species in the ecosystem leads to still another source of complexity: the overall system structure. There is a holistic school of thought, that regards systems as being more than the sum of their parts. According to this approach systems posses new properties, called emergent properties, which cannot be predicted from analyzing, no matter how precisely and completely, the component parts.

An offshoot of this second approach is the notion that biological systems are hierarchically organized, with new properties at each level of the hierarchy (Allen and Starr 1982, O'Neill et al. 1986). According to this view ecological complexity is better understood if ecosystems are decomposed hierarchically so that each process can be viewed as a stabilizing or disruptive factor at each level in a hierarchy of time and space scales. Furthermore, in this conception, biological systems are not solely the result of the interaction of their component parts, but lower levels in the hierarchy are constraint by phenomena occurring at higher levels.

Conceptualizing complex ecosystems as hierarchically organized systems facilitates their study. The critical task now becomes to identify the hyperplanes

in the space and time domains where discontinuities in system function occur and to specify the functional relationships among the levels. These discontinuities are supposed to represent the natural functional hierarchical structure of an ecosystem.

7.3.1. Hierarchy Theory

There are at least three meanings of biological hierarchies which has created a great deal of confusion. In the first place are taxonomic hierarchies. Hierarchies in this context are classificatory devices, that may or may not have biological meaning. All species that share certain characters are said to belong to a genus; all genera with certain attributes belong to the same family; and so on.

A second type of hierarchy in biology is a structural hierarchy. A tree is formed by roots, a trunk, and various orders of branches; each of these structures is formed by various types of tissues; each tissue by specialized cells; each cell type by a cell wall, membranes, cytoplasm, nucleus, etc. A structural hierarchy is supposed to represent real levels of complexity. There is some question, however, whether the structural levels that we recognize are not influenced more by our measuring abilities, than by intrinsic properties of the system.

A third kind of hierarchy is a functional or control hierarchy. According to this hypothesis, organisms are formed by stable subsystems organized into hierarchies for thermodynamic reasons. A system with such characteristics is supposed to be more stable and also capable of evolving.

A central tenet of the neo-Darwinian theory of evolution is that natural selection and genetic drift take place in species populations, and that consequently evolution cannot be explained by a reductionist approach. The attitude of some molecular and cell biologists (Lima-da-Faria 1988) has been exactly the opposite: they have sought to explain all of evolution as determined by the properties of molecules, genes, and cellular organelles. Lately a number of biologists and philosophers of science have questioned both these extreme points of view pointing out that natural selection and evolution can proceed at multiple levels (Lewontin, 1970; Wade 1978; Wilson 1980; Sober 1985. See also chapter 6 by P. Schuster).

By definition (Darwin 1964) natural selection affects a set of objects if there is heritable variation among them (see chapter by Schuster). A large number of biological units exist that fit this definition ranging from macromolecules and genes to cells, cell lineages, individual organisms, species, phyletic lineages, and possibly communities and ecosystems. Historical circumstances and the fact that it is easier for humans to identify with individual organisms has generated the conception that natural selection is purely a populational phenomenon. But if natural selection can proceed at many levels how is the process to be visualized and understood, especially when it is considered the force that directs the evolution of all living matter? Are we to assume that genes, cells, individuals, and species are evolving separately and not in concert?

The solution to this dilemma is to assume that there exists a hierarchy of components at different and discrete levels of organization (Allen & Starr, 1982; Salthe 1985). Units at a given level of organization are composed of elements belonging to a lower level, which in turn are composed by elements of a still lower level of organization, and so on. All units belonging to a given level are contained in the higher level, forming a nested hierarchy (fig. 7-6). A very important assumption of the theory is that units at different hierarchical levels do not interact in the same dynamic process, but constrain each other so that they set up the limits of actions of units at other levels. The interactions are most effective across contiguous levels. So, for example, the opening and closing of stomata in a leaf will directly affect the fluxes of gases in and out of a leaf and the rates of photosynthesis and transpiration, but is not going to affect the function of mRNA in the cells of the leaf other than through the action that a change in the rate of photosynthesis may have on the availability of high-energy bonds in the cellular environment, and how the availability of high-energy bonds affects protein synthesis.

A consequence of the hierarchical organization of natural units, is that a change at any one level of the hierarchy will be selected only if the change does not have a deleterious effect at a higher hierarchical level. So, for example, a mutation affecting the structure of a cell membrane and increasing its functional efficiency will be selected only if the mutated cell membrane does not constrain other functions of the cell; the modified cell does not constrain the function of the tissue and organ to which it belongs, and so on. The mutation can be rejected, even though the mutated membrane may have provided an advantage to the cell had it been a free living cell. On the other hand natural selection may favor a mutation eliminating chlorophyll from the cells of the petals of a flower

if it attracts more pollinating insects in spite that it reduces the efficiency of the petal cells as photosynthesizing organs. Such a mutation will not have been selected had the petal cells been free living cells.

Hierarchical theory has been applied to ecological systems (Allen and Starr 1982; Salthe 1985; O'Neill, et al. 1986). According to this view the environment can be ordered into a series of hierarchical levels each impinging on lower levels.
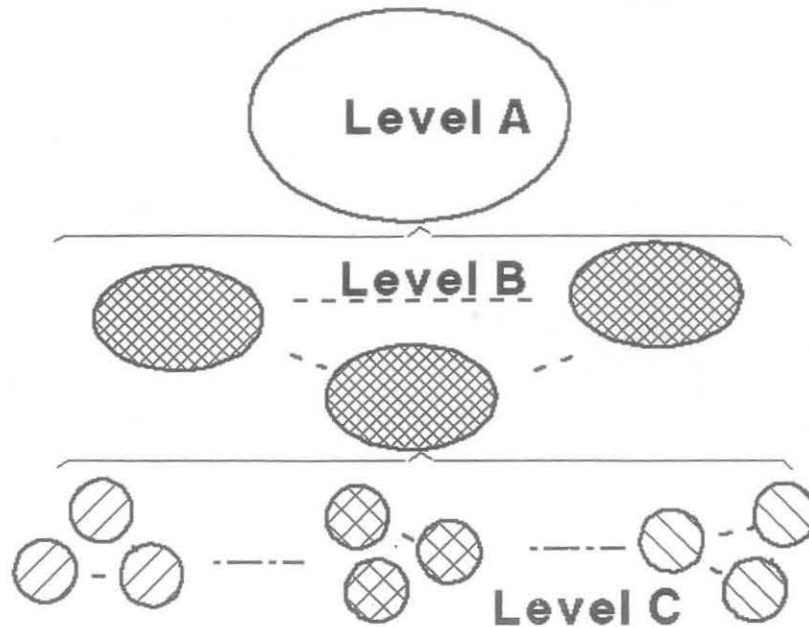

Figure 7-6. A sketch of a generalized hierarchical system. Thick arrows indicate strong interactions; broken arrows, weak interactions. Modified after Urban et al. 1987.

For example, the solar system would constitute a hierarchical level whose component parts would be the sun and the various planets. Certain relations between the sun and planets including the well known Milankovitch discontinuity affect the energy exchanges between Earth and Sun leading to cycles of low and high temperatures characterized by glacial and interglacial periods. In turn the changes in temperature (and associated changes in precipitation) create a diversity of climates in time that affect processes of soil formation, and geomorphological patterns. These in turn determine the type of vegetation in time and space, and serve as evolutionary selective agents. While changes in

the Earth's orbit around the sun have no direct effect on vegetation, immediate climate does. However, while the biological hierarchy is clearly nested, the environmental hierarchy is not. Rainfall affects such diverse processes as soil structure, degree of nutrient leaching, rates of decomposition, and plant transpiration, which clearly cannot be considered to belong to the same hierarchical level. This makes hierarchical theory more difficult to apply in ecology than in evolutionary studies.

Hierarchical theory is a very useful device to discipline the thoughts of the ecologist. By itself it does not provide any new insights. In identifying hierarchical levels the researcher can appreciate which phenomena or processes provide the mechanism that explain the function of the ecosystem at the level of interest, and which factor constrain the evolution of the system. Hierarchical theory also provides a vehicle that unites the populational and functional approaches to ecosystem studies.

Hierarchical theory has undoubtedly great heuristic value, especially for evolutionary studies. However its approach is static rather than dynamic, and the problem in such an approach lies in the risk of confusing the model with reality. I now consider the relation between biological complexity and environment in more detail.

7.4. ECOLOGICAL COMPLEXITY

At least three different hypothesis can be proposed to explain the complexity that we observe in ecosystems. One set of hypothesis suggests that the patterns of species that we observe at the ecosystem level are the resultant of interactions (such as competition, predation, comensalism, and symbiosis) between the species as they try to extract energy and resources from the environment. A second class of hypothesis explains the complexity of ecosystems as driven by interactions of species with the physical environment, such as rainfall patterns, fire frequency, intensity of frosts, etc. Finally a third hypothesis is that the observed patterns result from randomness in nature.

In previous sections we have shown how simple behavior (population growth, irrgular spatial patches) can generate complexity. Furthermore, the presence of organisms different capabilities and constraints creates a new level of complexity: that of the ecological community. The complexity of the ecosystem may accelerate the flow of energy and materials, increasing the standing

biomass of the component species, and create new and unique environments that species with still more specialized characteristics may exploit. So, for example, a unicellular photosynthesizing prokaryote can probably exist indefinitely by itself by fixing carbon and nitrogen it requires from the air while absorbing other nutrients from rainwater or its surroundings. Higher plants can fix carbon and absorb nutrients at a much higher rate than their prokaryote ancestors and create a much higher amount of standing biomass. However an angiosperm cannot exist indefinitely by itself because it cannot fix nitrogen, and its much higher nutrient requirement means that it will eventually exhaust the nutrients in the soil unless it coexists with organisms that decompose dead plant matter and return its elementary mineral ions back to the soil.

Environmental dependence is much more direct and constraining in the case of a free living cell than it is in a cell of a multicellular organism even though a multicellular organism is just as constrained by its environment as is a unicellular organism; likewise temperature affects the metabolic activity of a plant more directly than it does a homotherm animal. This is one direct result of the evolution of complexity. Complexity creates homeostasis at lower levels of the hierarchy, but not necessarily at the higher levels. Although a greater degree of complexity has allowed some organisms to overcome certain environmental constraints, it has excluded them from exploiting some other resources. So, for example, only multicellular organisms are capable of true locomotion or flight; but only unicellular prokaryotes are able to live in hot springs or reduce nitrogen.

In previous sections we have shown how very simple behavior (population growth, irregular spatial patches) can generate complexity. These examples do not exhaust all posibilities. The most intersting result of modern studies of complexity is that very deterministic dynamics of the form

$$dX_i/dt = F(X_i)$$

can give rise to very complex and apparently random behavior.

We tend to think that deterministic dynamics should give rise to invariant and predictable behavior. The field ecologist who observes the extremely variable and complicated face of nature has tended to attribute most variability to the indetermancy of nature. Since plants are so dependent on temperature, rainfall, and nutrients, it is tempting to attribute all variation to exterior factors.

As this brief analysis shows, some ecological complexity has its origin in extremely simple biological processes. How much is still an open question.

The investigation of the processes and mechanisms that originate complex patterns in ecosystems has not always been pursued with sufficient rigor. The existence of a pattern of complexity is not sufficient evidence for the operation of a process that creates and maintains that pattern since it can be the result of randomness. To prove that a pattern of complexity is not the result of randomness it must be shown that there is either a positive or negative correlation between the abundance of two or more species, or between the abundance of a species and a particular environmental factor. If such correlation exists, and if it is attributable to either competition for resources, or changes in survivorship, then the exact mechanism must be determined through the usual procedure of laboratory and field experimentation.

Complexity of ecosystems is not selected directly, but through mechanisms of interactions of the component species, not too!unlike than the case of cellular or organismic complexity. The difference is that in ecological units, the component species at a lower level of organization are free living, and all are not necessarily always present both in time and space. Once a complex ecological structure is in existence, natural selection acting on its component species, changes the nutrient and material cycling characteristics of the system. It is not entirely clear whether such a process increases the overall efficiency of materials and nutrient transfers. So, for example, plants in an ecosystem may adjust their chemical composition in response to attacks by insect herbivores. The change in the chemical composition of the vegetation may result in herbivores changing their digestive abilities to try to detoxify poisonous plant products. Likewise the decomposer microflora will evolve enzymes to function in the changed chemical environment of the litter. The overall result may be a lowered rate of nutrient cycling.

Ecosystem complexity differs in origin and maintenance from organismic complexity. The first and most important distinction is that ecosystems are not subjected to Darwinian natural selection in the same way that organisms are. There is no such thing as "ecosystem fitness," because there is no ecosystem offspring, only offspring of its component species, many or most of which make a living by reducing the fitness of their neighbors.

Another important difference is that the ecosystems are not bound in time by birth and death in the same way as individual organisms are. An ecosystem is formed by parts that are capable of independent existence. Consequently the ecosystem has no fixed temporal or spatial form. The parts of an ecosystem are interchangeable and replaceable. Unlike the individual organism, an ecosystem has no intrinsic limit to its longevity. Since it is not itself an organism, an ecosystem has no organic processes and hence no life cycle.

In brief ecological communities and ecosystems exhibit unique structure and function because each individual component is constrained in its behavior, but the ecosystem does not function as an organic whole, a superorganism. In a sense, and at a very different scale, an ecosystem is more like a complex biochemical system formed by interacting molecules, than like an evolving organism.

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